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Interspecific competition between resident and wintering birds: experimental evidence and consequences of coexistence

Luke L. Powell[1,2*], Elizabeth M. Ames[1,3], James R. Wright[1,3], Jason Matthiopoulos[4], and Peter P. Marra[1,5]

[1]Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological 7 Park, P.O. Box 37012, Washington, D.C. 20013-7012, USA.

[2]Current addresses: Institute of Animal Health and Comparative Medicine, University of Glasgow, Glasgow, G128QQ, UK and Department of Biosciences, Durham University, Stockton Road, Durham, DH13LE, UK.

[3]Current address: The Ohio State University, 210 Kottman Hall, 2021 Coffey Road, Columbus, OH 43210 USA.

[4]Institute of Animal Health and Comparative Medicine, University of Glasgow, Glasgow, G128QQ, UK.

[5]Current Address: Department of Biology and McCourt School of Public Policy, Georgetown University, 37th and O Streets NW, Washington, DC 20057, USA

*Correspondence. E-mail: Luke.L.Powell@gmail.com

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Abstract

The contribution of interspecific competition to structuring population and community dynamics remains controversial and poorly tested. Specifically, interspecific competition has long been thought to influence the structure of migrant-resident bird communities in winter, yet experimental evidence remains elusive. The arrival of billions of songbirds into Neotropical habitats, where they co-exist with residents, provides a unique opportunity to assess interspecific competition and its consequences. Working in 15 ha of Jamaican black mangrove forest, we used removal experiments to test whether dominant resident Yellow Warblers compete interspecifically with subordinate wintering American Redstarts; we also used observational evidence (interspecific territorial overlap) to understand whether this coexistence influences physical condition, spring departure dates or annual return rates. Consistent with interspecific competition, after experimental removal of the resident, yearling male redstarts (but not females or adult males) immediately into vacated Yellow Warbler territories, increasing their overlap with the space by 7.3%. Yearling redstarts also appeared to adjust their territorial space use by actively avoiding Yellow Warblers; for example, redstarts departing the wintering grounds as yearlings and returning the following winter shifted such that their territories overlapped 32% less with those of Yellow Warblers. Adult redstarts showed no such territorial flexibility. Adult male redstarts also showed evidence supporting the consequences of coexistence: territorial overlap with Yellow Warblers was negatively correlated with body condition and annual return rates. Adult male redstarts with <25% territorial overlap with Yellow Warblers were more than three times as likely to return between seasons than those with 100% overlap. We propose that the territorial inflexibility of adult male redstarts produces these consequences, which may be due to their years-long investment in that particular territory. More generally, the temporary nature of migrant-resident interspecific competition is likely what allows coexistence during winter, the most resource poor time of year. Our observations suggest that interspecific competition and the consequences of coexistence are age- and sex-specific and the product of intraspecific dominance hierarchy in redstarts. Our observations suggest that interspecific coexistence has measurable consequences, and our experiments support the long-held, but previously untested belief that resident birds compete interspecifically with wintering migrants.

Keywords: 3D territory mapping, Caribbean, Jamaica, migratory birds, Neotropical resident birds, redstart, warbler

INTRODUCTION

Despite much research, the importance of interspecific competition as a process shaping community structure remains controversial (Huston 1994, Hubbell 2008, Dhondt, 2012), due in part to challenges of producing rigorous experimental tests of the existence of competition as well as systematic evaluations of alternative hypotheses (Connell 1983, Schoener 1983, Martin & Martin 2001, Siepielski & McPeek 2010). It is important that we understand whether interspecific competition is operating in natural systems, because to effectively manage and conserve biodiversity, one must understand how populations, communities and ecosystems function (Dhondt 2012). For example, interspecific competition has long been thought to influence the structure of migrant-resident bird communities in winter (Ricklefs 1992), yet convincing experimental evidence for this competition remains elusive (Greenberg 1986, Greenberg & Marra 2005, Sherry et al. 2005, Toms 2013).

After the temperate breeding season ends, billions of migratory songbirds depart North America for the Neotropics, where they spend 6–8 months of the year (hereafter "winter") alongside ecologically similar year-round residents, creating ideal conditions for competition. When resources are limited, species with broadly overlapping ecological niches cannot coexist in equilibrium (Gause 1934, Hardin 1960); however, these species may weather temporary periods of limited resources and intense interspecific competition, with neither species going extinct but one or both experiencing fitness consequences (Hutchinson 1961, Kremer & Klausmeier 2017). The arrival of migratory birds to the Neotropics each winter can more than double the number of insectivorous birds in a given habitat (Buskirk & Buskirk 1976, Hespenheide 1980, Keast & Morton 1980). Paradoxically, this annual peak in songbird abundance eventually coincides with the tropical dry season and annual decline in arthropod abundance (Janzen 1973, Leisler 1992, Young 1994), maximizing the potential for competition between migrant and resident birds.

Jamaican mangrove forest is among the most-studied habitats in the context of non-breeding migratory bird ecology (e.g., Marra 2000, Powell et al., 2015). In Jamaican mangroves, wintering

migrants do not require nesting sites and avian predators of adult birds are rare (e.g., mortality of redstarts overwinter is <5%; Marra and Holmes 2001; P. Marra, pers. obs.), leaving food and space as the primary resources underlying migrant-resident competition. For insectivorous birds in this habitat, both space (mangrove trees) and insects (food) are distributed thinly but uniformly; resources are *not* patchy, as might be the case with fruiting trees. Under such uniform conditions, territoriality tends to be favored, because a territory-holding bird contains the food it needs to sustain itself within that territory (Brown 1964, Horn 1968). Thus, for insectivorous birds in Jamaican mangrove forest, individuals are highly territorial, with food and space tightly linked (Sherry 2005). Wintering American Redstarts (*Setophaga ruticilla*; hereafter "redstarts") show strong intraspecific interference competition; they aggressively chase conspecifics from their small territories (Marra 2000, Studds & Marra 2005). The high quality of these territories is due primarily to high arthropod availability relative to that of adjacent upland habitats, even in times of drought (Parrish & Sherry 1994, Studds & Marra 2007). Coexisting with redstarts in mangrove forest is an abundant year-round resident, the Yellow Warbler (*Setophaga petechia*), which is ecologically similar and phylogenetically related to redstarts (Lovette et al. 2010). Yellow Warblers, which are about 40% larger than redstarts, constantly show overt aggression towards wintering redstarts, both in Jamaica and elsewhere in the tropics (Greenberg & Ortiz 1994, Greenberg et al. 1996), suggesting that it exclude the smaller migrant from space. All 176 aggressive interactions between these two species observed on our study site were Yellow Warblers chasing redstarts of all age/sex classes—redstarts were never seen chasing Yellow Warblers (P. Marra, R. Dobbs & L. Powell, unpublished data from 2009, 2014 & 2015).

In addition to the challenges that most wintering migrants face in coexisting with residents, subordinates may not have equal access to resources due to intense *intra*specific competition. Although few empirical examples exist, the social dominance hypothesis predicts that subordinate age/sex classes should experience consequences associated with being relegated to relatively poor habitat (Catry et al. 2006, Mettke-Hofmann et al. 2015)—this pattern is conspicuous and well-studied in redstarts. In Jamaica, wintering adult male redstarts, which are behaviorally dominant over females and yearling males, select high quality mangrove habitat, forcing their female and yearling subordinates into low quality logwood habitat (Marra & Holmes 2001). Relative to redstarts in logwood habitat, individuals in high quality mangrove habitat tend to: 1) be in better physical

condition and lose less mass over the course of the winter season, 2) depart earlier on spring migration, 3) return at a higher rate in following winters, and, 4) have higher annual survival (Marra et al. 1998, Marra & Holmes 2001, Studds & Marra 2005, Johnson et al. 2006, Studds & Marra 2011). Collectively, these studies demonstrate strong consequences of intraspecific competition mediated through a social dominance hierarchy in redstarts: males are dominant over females, and adults (AKA "after second years") are generally dominant over yearlings (AKA "second years": 7-10 months old; Marra et al. 1993, Marra 2000). These consequences of competition are thought to lead to increased mortality, male-biased sex ratios (Breitwisch 1989, Villard et al. 1993, Marra & Holmes 1997), and interactions with competing species, all of which can influence population dynamics (Ricklefs 1992, Durell et al. 2001). Redstarts selecting wintering habitat must confront a critical tradeoff: low-quality logwood habitat that is free of Yellow Warblers or high-quality mangrove habitat in which they are constantly being chased by an aggressive, dominant species.

Three fundamental conditions must be demonstrated to "consider the existence of interspecific competition" (Weins 1989, Newton 1998, Dhondt 2012), all of which have been met in our study system. First, resources must be limiting. Three redstart removal experiments in this system have shown that space for territories (Marra et al. 1993, Marra 2000, Studds & Marra 2005) and food (arthropods) are both limiting (Cooper et al. 2015). Second, intraspecific competition must be documented, which has also been shown in redstarts through experimental (Marra et al. 1993, Studds & Marra 2005) and observational studies (Marra & Holmes 2001; Marra et al. 2015b). Third, resource use between potential competitors must overlap; this is clearly true for space as the typical Yellow Warbler's territory has at least six redstart territories overlapping it (R. Dobbs et al., unpublished data from 2009). The two species also have broadly overlapping diets on our study plots based on diet DNA metabarcoding from the winter of 2015 (Southwell 2018; n = 105 redstarts; n = 74; Yellow Warblers), suggesting the potential for exploitative competition.

Here, we test the hypothesis that interspecific competition occurs between wintering redstarts and resident Yellow Warblers within Jamaican mangrove forest. Based on the feasibility of the fieldwork required to test our predictions, we focused on documenting the negative effects of the dominant Yellow Warbler on the subordinate redstart (rather than vice versa), and we quantified resource overlap in terms of interference competition and territorial space rather than exploitative

competition and food *per se* (Brian 1956). We first use two-dimensional (2D) territory mapping to test the prediction that territorial overlap between redstarts and Yellow Warblers is dependent on sex and age classes of redstarts (Marra et al., 2000). We then used Yellow Warbler removal experiments combined with 3D territory mapping of both focal warbler species to test the prediction that redstarts are excluded from space by Yellow Warblers. Finally, we measure redstart mass loss, body condition, departure dates, and annual return rates to test the prediction that territorial overlap with Yellow Warblers has consequences associated with redstart fitness.

MATERIALS AND METHODS

Study Site

We conducted our study at the Font Hill Nature Preserve (18º02'N, 77º57'W; <5 m above sea level) at Luana Point, Jamaica, over three field seasons (January–April of 2014–2016). Average monthly rainfall exceeds 100 mm from August to November but drops to <25 mm from December through May (Jamaican Meteorological Service, unpublished data). Mangrove habitat consists of a ~12-m tall closed-canopy mature forest dominated by black mangrove (*Avicennia germinans*). Importantly, by century's end, the global extent of mangrove is projected to decrease by 10-15% due to lea level rise associated with climate change, and by 1-2% *per year* from deforestation (Alongi 2008). See Marra & Holmes (2001) for a complete description of the study area.

Study Species

Although other small insectivores are present in our study system, we focused on redstarts and Yellow Warblers because they are the most common and most territorial species present, and also tend to show the most interspecific aggression (i.e., are the most likely to compete). Redstarts are 6-9g insectivorous songbirds found in myriad habitats, with evergreen mangrove forests being of highest quality in our study area (Marra & Holmes 2001, Studds & Marra 2005). Redstarts hold very small individual territories (~0.18ha; often as few as ~4-5 trees) that they defend against conspecifics. Adult males have bold black-and-orange plumage, whereas females and yearling males are dull gray. Co-occurring with redstarts in the mangrove is an abundant year-round resident, the "Golden" subspecies

of Yellow Warbler (9-12g; *S. p. eoa*). In Jamaica, Yellow Warbler pairs defend territories more than three times larger (~0.6 ha) than those of redstarts. In Jamaican mangrove, Yellow Warblers interact far more with redstarts than with the other common songbirds; these include the resident Jamaican White-eyed Vireo (*Vireo modestus*), and migrant Black and White Warbler (*Mniotilta varia*), Black-throated Blue Warbler (*S. caerulescens*), Northern Parula (*S. americana*), Northern Waterthrush (*Parkesia noveboracensis*), and Prairie Warbler (*S. discolor*).

Territory mapping

We used two methods to map color-banded redstart and Yellow Warbler territories: a two-dimensional (2D) method used over the extent of each field season, and a high-resolution but labor intensive three-dimensional method (3D; adding height; Cooper et al. 2014) used during Yellow Warbler removal experiments.

2D Territory mapping

We captured, measured and color-banded redstarts and Yellow Warblers using techniques detailed in Marra & Holmes (2001). Territories were 2D-mapped on three 5-ha mangrove study plots during Jan-Mar of 2014–2016. Each gridded plot was mapped daily (~7 hrs) by an average of two technicians, resulting in >50 observations for most individuals. We created individual summary maps following Marra et al. (2015b; see supporting information). To quantify interspecific territorial overlap between redstarts and Yellow Warblers as measured in 2D (hereafter "2D overlap"), we converted summary territory maps to digital polygons and used QGIS (2015) to calculate the proportion of each redstart territory that overlapped with a Yellow Warbler territory as well of the extent of redstart territories in logwood habitat. As Yellow Warblers do not inhabit logwood habitat, we excluded redstarts having >30% of their territories in logwood habitat and individuals in areas in which Yellow Warbler territories were not precisely mapped due to high water containing American Crocodiles (*Crocodylus acutus*).

3D Territory Mapping

To determine how space use changes for redstarts when Yellow Warblers are removed, we mapped

individuals' movements in 3D. We tracked individuals by following them with a numbered set of flags, with each flag representing a bird location at 30 second intervals. As we followed, we recorded range-finder-calibrated bird height and flag number on a voice recorder, only dropping flags after birds moved ≥10m from the observer. 3D territory maps were considered complete after flagging approximately 90 locations because this is the point at which 3D territory sizes of redstarts in our study tend to reach an asymptote (Cooper et al. 2014). We then used a Trimble GPS (error = 1.2m) to mark locations of the flags and transcribed height data from the recorder. See supporting information for more detail.

Interspecific 2D overlap among redstart age/sex classes

We ran generalized mixed models in program R to determine if proportional 2D overlap between individual redstart and any intersecting Yellow Warbler territories (response or dependent variables) varied with age and sex of redstarts as well as year (fixed effects or independent variables). We logit-transformed 2D overlap (Warton & Hui 2011) and used individual redstart as a random effect on the intercept to capture individual variation. We fit 10 candidate models (Appendix S1: tables). Because several well-supported models emerged from model selection, we performed model averaging using the R package "MuMIn" using the 95% confidence set of models, then based conclusions on model-averaged predictions.

For this and all other mixed models, we based conclusions on model selection as well as line, point and 95% confidence interval estimates generated from the most parsimonious model or the results of model averaging (Burnham & Anderson 2002). We checked fit of the best-fit models upon which we based conclusions by calculating the marginal r^2 for generalized mixed models (the variance explained by the fixed effects; Nakagawa & Schielzeth 2013; R package "MuMIn"). Additional statistical methods and candidate model sets are available in Appendix S1.

Change in 2D overlap between seasons

To determine whether redstarts returning between winters shifted their territories with respect to Yellow Warbler territories, we examined between-season change in 2D overlap for 43 redstarts returning in successive seasons (2014–2015; 2015–2016). We ran 7 normal candidate mixed models

with individual redstart as a random effect on the intercept to determine if between-season change in 2D overlap (overlap in year t – overlap in year t + 1; dependent variables) varied by redstart age, sex, and year (independent variables).

Yellow Warbler removal experiment

We experimentally removed Yellow Warblers from the territories of 31 redstarts across two winters (2014 and 2015). We either permanently (n = 12 territories) or temporarily (n= 17) removed all territorial Yellow Warblers (both males and females; see supplements) from focal redstart territories. Immediately after Yellow Warblers were removed, we 3D-mapped space use by redstarts whose territories overlapped those of the removed Yellow Warblers. For the permanent removal subset, we performed control mapping by tracking redstarts and Yellow Warblers a few days prior to the removal experiment. We then permanently removed all territorial Yellow Warblers and commenced the experimental mapping of redstarts in the absence of Yellow Warblers. For temporary removals, we captured all territorial Yellow Warblers, put them in a cage for several hours, and performed experimental mapping of redstarts. We then we waited ~40 hours post-release to allow Yellow Warblers to recover from the removal experiment, and then performed control mapping. All Yellow Warblers returned to defend their territories by 40 hours post removal.

For both temporary and permanent removal experiments, we 3D-mapped the same redstarts from the removal day as well as the overlapping territorial adult Yellow Warblers. For redstarts, we used the same mapping technique on the experimental and control days, taking care to track individuals for approximately the same amount of time as during the removal tracking. For Yellow Warblers, we considered joint territories of the male and female Yellow Warblers, gathering a minimum of 90 locations per territory and 30 per bird. We ended experiments when approximately 90 locations were recorded for each focal redstart; experiments lasted 3.4 hours on average (min: 1.5h, max: 4.8h).

We calculated 3D utilization via kernel smoothing, using the R package "ks" (Duong 2007; see supplements). We defined territory as the 95% utilization distribution of the kernel density estimator and core territory as the 50%. Because an animal's core area is considered the most important part of its home range—where it concentrates its space use (Seaman & Powell 1990)—we

expected this space to be the most vigorously defended, and thus defined overlap as the degree to which the redstart territory overlapped with the Yellow Warblers core territory (hereafter "3D overlap"). To analyze how redstarts responded to the experimental removal of Yellow Warblers, we developed 7 normal generalized linear candidate models, including plausible combinations and interactions among year, redstart age and sex, as independent variables. Our dependent variable was the difference in interspecific 3D overlap between experimental and control treatments, i.e., proportion of redstart 3D overlap with (vacant) Yellow Warbler core territory during the removal experiment *minus* proportion of redstart 3D overlap with (occupied) Yellow Warbler core territory during the control.

Consequences of 2D overlap for redstarts

Mass loss vs. 2D overlap

We captured 16 redstarts in both early and late winter to quantify within-season mass change (see supplements). We ran 15 normal candidate generalized linear models to determine if mass change (dependent variable) varied by year and redstart age, sex, and 2D overlap (independent variables). No redstarts were repeated within this analysis, so we did not include the random effect of individual redstart.

Body Condition vs. 2D overlap

To estimate redstart body condition, we calculated a scaled body mass index (residuals of mass regressed on tarsus length; hereafter "body condition"; Peig & Green 2009; see supplements). We then ran 15 normal candidate mixed models with individual redstart as a random effect on the intercept to determine if body condition (dependent variable) varied by redstart age, sex, year, and 2D overlap (independent variables).

Departure date vs. 2D overlap

We determined departure date for each redstart following Marra et al. (1998) and Studds & Marra (2011), searching for territories every 3 days from 1 April to 15 May (see supplements). We ran 15 normal candidate mixed models with individual redstart as a random effect on the intercept to

determine if departure date (dependent variable) varied by redstart age, sex, year, and 2D overlap (independent variables). Because several well-supported models emerged from model selection (some of which included overlap, the main variable of interest), we performed model averaging using the R package "MuMIn" using the 95% confidence set of models, then based conclusions on model-averaged predictions.

Between-season returns vs. 2D overlap

We first determined if a color-marked redstart was present in our plots during a given winter season using a combination of banding records, sightings during the hundreds of hours of 2D territorial mapping and records from the departure protocol (Marra et al. 1998). We then ran 16 candidate mixed logistic models with individual redstart as a random effect on the intercept to determine if the probability of returning between seasons (dependent variable) varied by redstart age, sex, year, and 2D overlap (independent variables). Due to variance in age/sex classes other than adult males, this combined modeling effort was poorly supported (i.e., the null model was most parsimonious). As such, we ran 5 candidate mixed logistic models on adult males only to determine if the probability of returning between seasons varied by year and 2D interspecific overlap.

RESULTS

Interspecific territory overlap among age/sex classes

An average of 8.25 (± 0.35 SE) redstart territories overlapped each Yellow Warbler pair's territory. Despite considerable variance, best-fit models showed that yearling redstarts had about 12% greater 2D overlap with Yellow Warblers than their adult counterparts ($r^2 = 0.04$; Adults: mean = 0.43, 95% CI: 0.22–0.66; yearlings: mean = 0.54, 95% CI: 0.30–0.76, Appendix S1: Fig. S1; see Table 1 for summary of results). No clear best-fit model emerged, but the 95% candidate set of best-fit models all included redstart age, and all models in this set outperformed both the null model ($\Delta AIC_c > 19$) as well as univariate models of sex or year ($\Delta AIC_c > 17$; Appendix S1: Tables S1 & S2).

Change in 2D territory overlap between winters

We detected thirty-three redstarts returning to our study area in two consecutive winters; 10 returned in three consecutive winters. We found a strong effect of redstart age on change in 2D overlap for individuals returning between winters (r^2 = 0.10; Appendix S1: Table S3). Redstarts departing as yearlings and returning as adults shifted their territories away from Yellow Warblers by 32% (95% CI: -0.32 ± 0.15); adults returning between winters showed little change in 2D overlap (95% CI: 0.019 ± 0.12; Fig. 1).

Yellow warbler removal experiment

The direction and magnitude of change in 3D overlap before vs. after Yellow Warbler removal varied with redstart age & sex (best-fit model: age * sex; r^2 = 0.36; Appendix S1: Table S4; Fig. 2). Yearling male redstarts (but no other age/sex classes) moved into the space vacated by Yellow Warblers, thus increasing 3D overlap with the Yellow Warblers' (vacated) core territory by 7.3% (e.g., Fig. 3, Video S1), and supporting our prediction that redstarts are excluded from space by Yellow Warblers. We found a weak trend ("significant" only with 80% CIs) of yearling females moving away from the space vacated by Yellow Warblers (Fig. 2).

Consequences of coexistence

Mass loss and body condition and 2D overlap

Interspecific 2D overlap was not correlated with within-winter redstart mass change; rather, the null model was best supported (Appendix S1: Table S5 & Fig. S2). Conversely, redstart body condition was influenced by 2D overlap with Yellow Warbler territories as well as redstart demography (best-fit model: age * sex * 2D overlap; r^2 = 0.32; Appendix S1: Table S6). Specifically, both the magnitude and the slope of the relationship between 2D overlap and redstart body condition varied by age and sex of redstarts (Fig. 4). In the relative absence of Yellow Warblers (< approximately 35% 2D overlap), adult male redstarts were in better body condition than all other age-sex classes (Fig. 4). Consistent with consequences of coexistence, the body condition of adult male redstarts declined as territorial overlap with Yellow Warblers increased. Based on the 95% confidence intervals, 2D overlap was not correlated with body condition for any other age/sex class; however, we found a marginal trend ("significant" only with 90% CIs) of

the body condition of yearling female redstarts increasing as territorial overlap with Yellow Warblers increased (Fig. 4).

Departure date and 2D overlap

2D overlap was not meaningfully correlated with departure date. The univariate model containing 2D overlap received less support than the null model, and the model-averaged parameter estimates showed at best trivial relationships between departure date and 2D overlap (Appendix S1: Figs. S3, Table S7 & S8). Although there was considerable variance, males appeared to depart prior to females and adults appeared to depart prior to yearlings.

Annual return rate and interspecific 2D overlap

When we modeled adult male redstarts only, 2D overlap was negatively correlated with return rate between winters (Fig. 5; Appendix S1: Table S9 & Fig. S4b; $r^2 = 0.25$). The best-fit model showed that adult males with <25% 2D overlap with Yellow Warblers were more than three times as likely to return between seasons (94%) than redstarts with complete 2D overlap (29%). We found essentially no correlation between 2D overlap and the return rate of yearlings or adult females: models of annual return rate with all age/sex classes combined received little support, with small sample sizes and large variation in 2D overlap for age/sex classes other than adult males (Appendix S1: Fig. S4a & Table S10).

DISCUSSION

We provided experimental evidence that resident Yellow Warblers compete with wintering migratory redstarts (*sensu* Dhondt 2012): yearling males moved into territorial vacancies created by the removal of Yellow Warblers. Furthermore, we provided observational evidence suggesting that redstarts show consequences of cohabitation with Yellow Warblers: adult male redstarts with high 2D overlap with Yellow Warblers were in poorer body condition and had a lower probability of return between winters than redstarts with low 2D overlap. Our results hint at another potential layer of intraspecific competition in which adult male redstarts that are inherently less fit are forced, through interference competition by other redstarts, to settle in territories overlapping greatly with Yellow Warblers. Under

these conditions, less-fit males might also suffer the effects of interspecific competition through both interference (aggressive chasing) and exploitation (reduction of food) by the dominant species, producing consequences such as those we observed: low return rates and reduced body condition.

Evidence for interspecific competition

Once the three fundamental conditions are met to "consider the existence of interspecific competition" (see introduction), *any* of three additional conditions support the existence of interspecific competition (Weins 1989, Newton 1998, Dhondt 2012), two of which we demonstrated in this study. First, resource use of one species must affect resource use of another species, which we found when yearling males redstarts shifted their territories into the spatial vacancy created through experimental removal of Yellow Warblers (Figs. 2 & 3). Second, the fitness of one species must be reduced by the presence of another; our results suggest this by demonstrating that adult male redstarts with higher territorial overlap with Yellow Warblers had reduced body condition (Fig. 4) and lower annual return rates compared to redstarts with less overlap (Fig. 5). We did not directly address the third condition, which states that the distribution or abundance of one species is reduced by another. Although Yellow Warblers spend considerable time and energy chasing redstarts many times per day, and this energy expenditure likely has consequences for Yellow Warblers, we did not quantify competition in this direction because, among other logistical challenges, it was not feasible to simultaneously capture and remove all the redstarts (mean = 8.25) from a given Yellow Warbler territory.

Variation in response to Yellow Warblers among redstart males

Yearling male redstarts appeared to be released from competition during removal of Yellow Warblers (Fig. 2), but it was adult males, not yearlings, that showed the apparent consequences of 2D overlap in terms of reduced body condition and return rates (Figs 4 & 5). This pattern requires careful interpretation. First, yearling territories overlapped more with Yellow Warblers overall (Appendix S1: Fig. S1), so we suspect they had more resources to gain when the competitor was removed. Second, yearlings may be more flexible in their resource use: theory and empirical tests suggest that social subordinates must either shift to a wider realized niche (Morse 1974) or use inferior resources to allow

interspecific coexistence (Pimm et al. 1985). This pattern probably plays out intraspecifically as well: yearling redstarts may be pushed by conspecific adults into an inferior habitat—one with less food that is aggressively defended by Yellow Warblers. As yearlings mature and ascend the redstart social hierarchy, they are likely in a better position to select and defend territories in superior habitat—this may be what enables them to shift territories between years (Fig. 1). Conversely, adult male redstarts did not adjust territories between winters (Fig. 1), during our removal experiments (Fig. 2) or after Cooper et al. (2015) reduced their food by 80% with insecticide. Over the course of the winter, adult male redstart territories lose less insect biomass than those of their yearling counterparts—especially during drought (N. Cooper, T. Sherry and P. Marra, unpublished data from 2010-2012), so when adjacent Yellow Warbler free space does become available, experience likely suggests staying put and sacrificing short term benefit for long term stability (Harvey et al. 1984, Holmes et al. 1996).

Contrary to what would be predicted from the social dominance hypothesis (Catry et al. 2006), adult males appeared to suffer the consequences of territorial overlap with the resident in terms of reduced body condition and return rates, but yearlings did not (Figures 4, S3 & S4). The most likely explanation is that adult male redstarts, the dominant age-sex class, also defended the highest quality territories (i.e., highest food availability and stability; Marra et al. 1993), which made them targets of interspecific aggression by Yellow Warblers with broadly overlapping diets (Southwell 2017). The relative spatial flexibility of yearling males (Figures 1 & 2) may make them less vulnerable to the consequences of cohabitation with the resident. A non-mutually exclusive alternative explanation is that the delayed plumage maturation of yearling males advertises their subordinate stature (Rohwer & Butcher 1988), resulting in reduced rates of aggression from both conspecifics (Järvi & Bakken 1984) and Yellow Warblers, thus increasing foraging rates (Rohwer & Ewald 1981) and body condition.

Yearling female redstarts: Benefitting from the presence of the resident?

In contrast to redstart males, subordinate yearling female redstarts may employ a very different strategy for coping with residents. Based on strict 95% confidence intervals alone, we detected no trend of yearling females responding to Yellow Warbler presence or removal. However, more liberal confidence intervals show a marginal pattern of yearling females moving *away* from the space vacated by removed Yellow Warblers (Fig 2; “significant” with 80% confidence intervals), and a

positive correlation between 2D overlap and body condition (Fig 4b; "significant" with 90% confidence intervals), hinting that they may benefit from the presence of Yellow Warblers. Our best explanation is that Yellow Warblers in Jamaican mangrove provide an otherwise unavailable niche for yearling females in high-quality wintering habitat—one that is relatively free of dominant conspecific competitors. Yearling females have duller plumage (Osmond et al. 2013), are smaller and less conspicuous than other age/sex classes (i.e., less bold, skulkier; L. Powell, pers. obs.), all of which may allow young females to use high-quality habitat and reduce intraspecific competition. The generality of these patterns was limited by the sample size of yearling females, which because they are subordinate, are often forced from mangrove into the relatively poor logwood habitat. (Fig. 2; Fig. 4b).

Ecological implications of variation in interspecific competition

Previous work from our study system showed that conditions during one phase of a migratory animal's life cycle carryover to affect fitness in subsequent phases (Marra et al. 1998, Marra & Holmes 2001, Reudink et al. 2009). Ricklefs (1992) argued that if migrant and resident populations even partially influence each other's population processes (i.e., are "coupled"), as our data strongly suggest, then the competing species should be considered part of a "megapopulation", in which evolutionary adjustments, niche, population dynamics and habitat selection are interdependent. Ricklefs (1992) hypothesized that migrant-resident coupling is most likely to occur among species ecologically or morphologically similar to each other, as with our focal species. Our findings add to the growing body of evidence on the importance of understanding the full annual cycle biology of migratory animals (Hostetler et al. 2015, Marra et al. 2015a). To fully estimate the challenges presented to migrants, full annual-cycle population models should incorporate competition from resident species during the non-breeding season.

The temporary nature of migrant-resident interspecific competition is what may allow coexistence during the most resource poor time of year. As shown both empirically and theoretically with planktonic as well as other systems, temporal fluctuations in resources (e.g., food) and competitor abundance can permit coexistence (Hutchinson 1961, Long et al. 2007) that may be stable over evolutionary time (Kremer et al. 2017, Miller & Klausmeier et al. 2017). The competitive exclusion principle assumes equilibrium (Hardin 1960), but during winter, these temporarily

coexisting songbird populations are *not* in equilibrium: for example, some mortality takes place but no young are produced. However, once migrants depart for the breeding grounds, both migrants and residents are essentially released from competition and immediately begin raising young (Raffaele 1998, Reudink et al. 2009). Further, although food is scarce and probable competitors are abundant during winter, two extremely demanding physiological processes, molting and breeding, are effectively avoided (Raffaele 1998), so both migrants and residents can probably make do with less food and of poorer quality (Greenberg 1995, Johnson et al. 2005).

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SUPPORTING INFORMATION

Additional supporting information may be found online at: [link to be added in production].

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SUPPORTING INFORMATION

Additional Supporting Information (may be downloaded via the online version of this article.

TABLE

Table 1. Summary of analyses and results for each age and sex class of American Redstarts relative to a dominant competitor, the Yellow Warbler ("yellow").

Analysis	Adult male	Adult female	Yearling male	Yearling female
Distribution vs. *2D overlap w/ yellow	less overlap	less overlap	more overlap	more overlap
Change in 2D overlap w/ yellow b/w seasons	†-	-	moved away	moved away
Territory shift relative to yellow core territory during yellow removal (measured in 3D)	-	-	moved in	moved away?‡
Departure date vs. 2D overlap w/ yellow	-	-	-	-
Mass change vs. 2D overlap w/ yellow	-	-	-	-
Body condition vs. 2D overlap w/ yellow	negative	-	-	positive?
Returning birds vs. 2D overlap w/ yellow	less overlap	-	-	-

* "2D overlap": Interspecific territorial overlap between American Redstarts and Yellow Warblers as measured in 2 dimensions.

†: "-" : no relationship detected

‡: Question mark indicates a weak pattern, i.e., only "significant" using 80-90% confidence intervals.

Fig. 1. Predicted change in 2D overlap of redstart and Yellow Warbler territories for restarts that returned between consecutive years. Numbers in bars indicate number of birds studied between-winters. Adults refers to birds that were already >1 year old in winter 1 and returned as >2 years old in winter 2; "yearlings" were <1 year old in winter 1 and returned as adults in winter 2.

Fig. 2. Predicted change in 3D overlap of American Redstart territories with the Yellow Warbler pair's core area during experimental removal of Yellow Warblers relative to control. Positive values indicate that American Redstarts increased overlap with the Yellow Warbler's core area during removal and vice versa. A = adult; Y = yearling. Sample sizes (number of birds) above bars.

Fig. 3. Territorial response of a yearling male American Redstart to removal of a Yellow Warbler pair, mapped in 3D, as viewed from a) above and b) the side. Yellow shapes: core territory of Yellow Warbler pair (created w/ $n = 83$ points). Gray shapes and points: redstart territory before Yellow Warbler removal ($n = 74$ points). Blue shapes and points: redstart territory after Yellow Warbler removal ($n = 83$ points). Scale of height is expanded to better visualize this dimension.

Fig. 4. Predicted body condition of male (a) and (b) female redstarts relative to 2D overlap of territories of American Redstarts with territories of Yellow Warblers. A = adult (darker colors and shading); Y = yearling (lighter colors and shading). Numbers indicate number of observations per age/sex class. Data points indicate raw (not predicted) values.

Fig. 5. Predicted probability of apparent return (returned + detected) of adult male American Redstarts (n = 32) between winters relative to proportion 2D overlap with Yellow Warbler territories. Includes data from 2014-2015 and 2015-2016. Data points denote raw (not predicted) values of whether or not birds returned (1) or not (0).

Figure 1

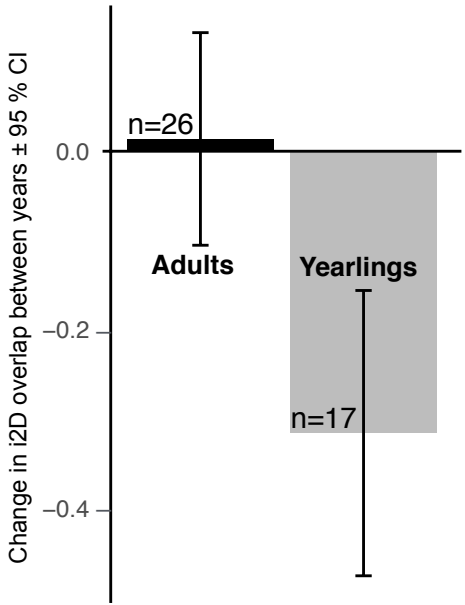

Change in i2D overlap between years ± 95 % CI
0.0
−0.2
−0.4
n=26
Adults
Yearlings
n=17

Figure 2

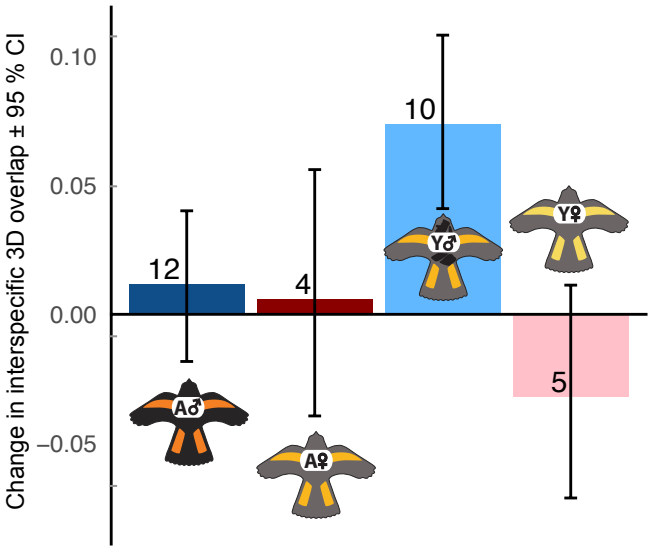

Change in interspecific 3D overlap ± 95 % CI
0.10
0.05
0.00
−0.05
12
4
10
5
A♂
A♀
Y♂
Y♀

Figure 3

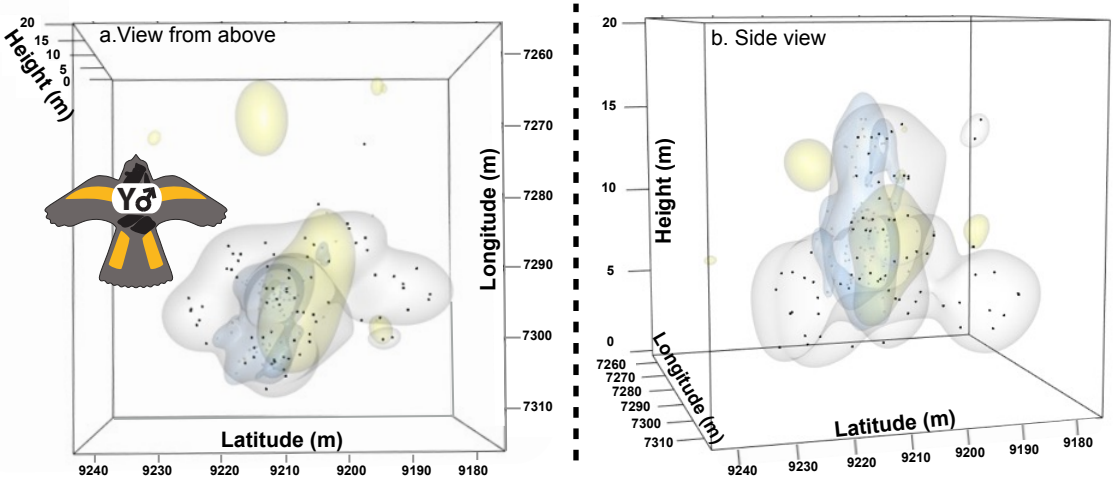

a.View from above
Height (m)
20
15
10
5
0
Longitude (m)
7260
7270
7280
7290
7300
7310
Latitude (m)
9240
9230
9220
9210
9200
9190
9180
b. Side view
Height (m)
20
15
10
5
0
Longitude (m)
7260
7270
7280
7290
7300
7310
Latitude (m)
9240
9230
9220
9210
9200
9190
9180

Figure 4

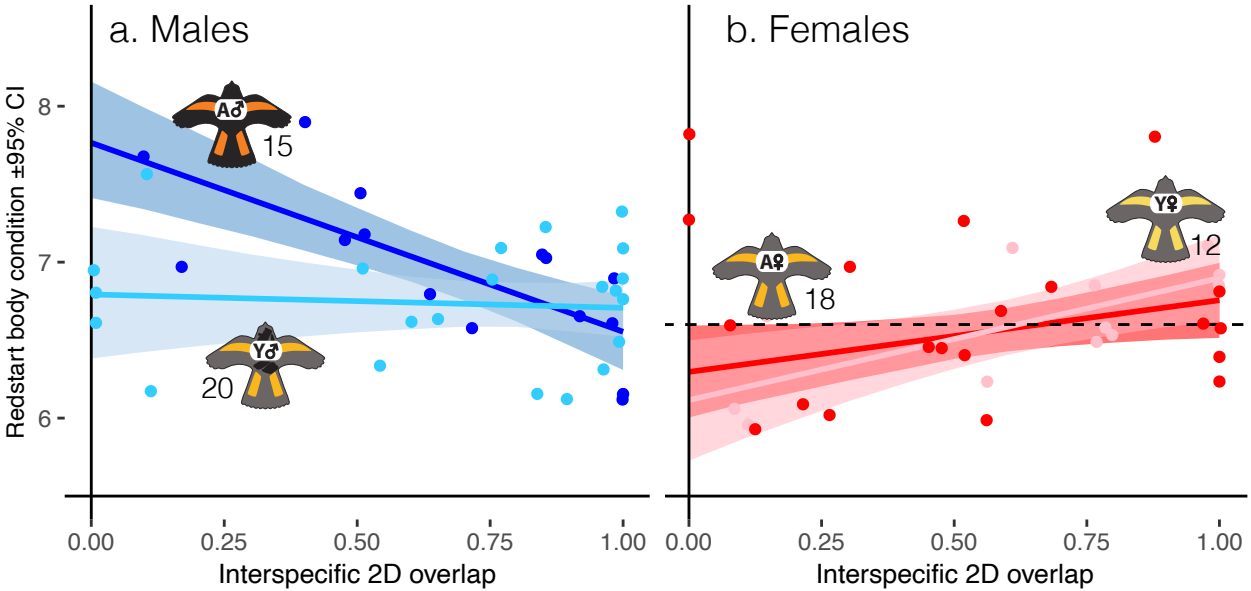
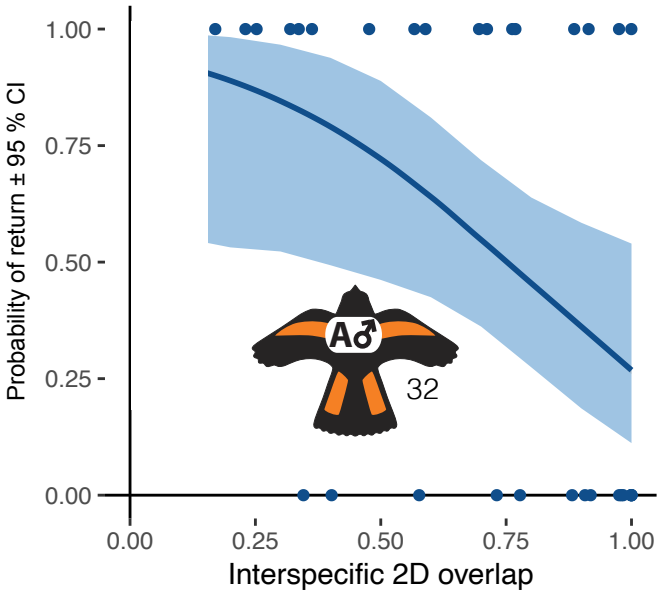

a. Males
b. Females
Redstart body condition ±95% CI
8
7
6
A♂
15
Y♂
20
A♀
18
Y♀
12
0.00
0.25
0.50
0.75
1.00
Interspecific 2D overlap
Interspecific 2D overlap

Figure 5


Probability of return ± 95 % CI
1.00
0.75
0.50
0.25
0.00
0.00
0.25
0.50
0.75
1.00
Interspecific 2D overlap
A♂
32